
*An Ethological Study of Certain Mal-
Adjustments in the Relations of
Ants to Plants.*

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Article XXIV.—AN ETHOLOGICAL STUDY OF CERTAIN MAL-
ADJUSTMENTS IN THE RELATIONS OF
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PLATES LXIII-LXVIII.

Much has been written concerning the mutual helpfulness of certain species of ants and plants, but very little attention has been bestowed on the cases in which these organisms live together in a state of imperfect adaptation or antagonism. And yet such conditions may be expected to exist as the preliminary stage, if nothing more, in the course of development leading to such complete and harmonious adjustments as we witness in the symbiosis of certain ants, like the American *Attii*, with the fungi which they not only systematically cultivate but carefully transmit from mother to daughter colonies generation after generation. In the following article I have collected a few cases which seem to me clearly to prove the existence of a struggle between the ants and their plant environment, a struggle in which the ants, notwithstanding their notorious adroitness in surmounting obstacles to their welfare, seem always to succumb.

I. THE MOUND-BUILDING ANT AND THE HAIR-CAP MOSS.

Some months ago Mr. W. D. W. Miller of the American Museum of Natural History called my attention to a beautiful colony of the mound-building ant of the Alleghenies (*Formica exsectoides*) near Scotch Plains, New Jersey. This colony, which Mr. Miller visited with me during May and June, is situated in a wood on flat clayey soil, at an altitude of about 150 meters. The nests, forty to fifty in number, are scattered over an area of less than a square kilometer and are all built in open, sunny clearings among the trees. There are nests in all stages of growth, from their first inception to old extinct mounds covered with moss and other plants. The worker ants, in full possession of the surrounding woods, are everywhere to be seen, running about on the ground in search of dead and disabled insects, and climbing the trees and bushes for the purpose of collecting the honey-dew from the droves of aphids and membracids. Though less numerous, the nests near Scotch Plains compare very favorably in size with those of the famous colony near Hollidaysburg, Penn-

sylvania, described nearly thirty years ago by McCook.¹ With the aid of my assistant, Mr. Roy E. Miner, I measured eleven of the largest mounds and record their height, transverse diameter through the base and over the summit and the circumference in meters and in feet, in the following table:

No.	Height.			Basal Diameter			Diameter over Summit.			Circumference.		
	m.	ft.	in.	m.	ft.	in.	m.	ft.	in.	m.	ft.	in.
1.	.90	2	11.3	1.40	4	6.9	1.91	6	2.9	4.398	14	4.4
2.	.77	2	6.2	2.65	8	7.9	2.85	9	3.7	8.325	27	2.4
3.	.48	1	6.8	2.23	7	3.4	2.61	8	6.3	7.005	22	10.6
4.	.77	2	6.2	2.36	7	8.5	2.64	8	7.4	7.414	24	2.6
5.	.85	2	9.3	2.45	8	.04	2.92	9	6.5	7.696	25	1.6
6.	.95	3	1.2	3.61	11	9.5	4.00	13	.8	11.341	37	.6
7.	1.00	3	3.2	3.25	10	7.4	3.84	12	6.5	10.21	33	4.2
8.	.70	2	3.4	2.46	8	.4	2.61	8	6.3	7.728	25	3.
9.	.58	1	10.7	1.79	5	10.2	2.12	6	11.1	5.623	18	4.4
10.	.80	2	7.4	2.23	7	3.4	2.53	8	3.2	7.005	22	10.6
11.	.73	2	4.6	2.04	6	.10	2.43	7	11.3	6.408	20	11.2

The average height of these mounds is .78 m. (2 ft. 6.5 in.) with a basal diameter of 2.40 m. (7 ft. 10 in.), a convex diameter of 2.77 m. (9 ft. 5 in.) and a circumference of 7.55 m. (24 ft. 7.9 in.). They exhibit considerable differences in shape, some being more pointed or conical, others more depressed and rounded. Although unusually well developed, none of these hills reaches the dimensions of one measured by McCook (*l. c.*, p. 255). This, the largest on record, was 1.07 m. (3 ft. 6 in.) in height, 7.34 m. (24 ft.) in diameter over the summit, and 17.75 m. (58 ft.) in circumference.

The mounds of *F. exsectoides* undoubtedly answer the same purpose as those of *F. rufa* in Europe and certain of its varieties in this country. As Forel has shown, these accumulations of detritus serve as incubators for the brood, since their temperature during the day is, of course, much higher than that of the underground portions of the nests. Unlike the mounds of *F. rufa*, however, those of *F. exsectoides* consist very largely of earth and only to a very limited extent of vegetable detritus and pebbles. McCook is certainly in error when he writes (*l. c.*, p. 270) that "every hill furnishes a fair measure of the extent of the underground system of galleries connected therewith; for it is reasonably certain that the entire bulk of soil in each mound has been excavated and brought from the galleries beneath the sur-

¹ Mound-building Ants of the Alleghenies. Trans. Am. Entom. Soc., VI, 1877, pp. 253-296, pls. ii-vi, 13 text-figs.

face." On the contrary, it is probable that much of the earthen material of the mounds, like all the vegetable detritus, is collected by the foraging workers from the surface of the area surrounding the nest. This material is brought together and built into the mound in the very same manner as the harvesting ants *Pogonomyrmex barbatus* and *P. occidentalis* collect their pebbles, and *F. rufa* its vegetable detritus. The interior of the mound of all these ants is riddled with galleries in which the larvæ and pupæ can be kept during the warm hours of the day for the purpose of accelerating their development.

It is not only an easy matter to observe any of our mound-making ants in the act of picking up and carrying materials to its nest, but the nature of the materials in certain localities is indisputable proof of such activity. Along the railroad tracks through Indiana, Ohio, and western New York, may be seen dozens of mounds of *F. fusca* var. *subsericea* covered with a thick layer of locomotive cinders that have been carefully collected by the worker ants. Even more striking is the same habit in *Pogonomyrmex barbatus* var. *molefaciens* along the railways of Texas, and in *P. occidentalis* in similar situations in Colorado and New Mexico. The large nest cones are often so black with cinders as to stand out in very sharp contrast with the pale surrounding soil. Along the Chicago, Burlington & Quincy R. R. for many miles east of Denver, Colorado, the nest cones of *occidentalis* close to the track are deep black, while those further away, to a distance of about thirty or forty meters, show a gradual fading in color, with the decrease in available cinders, to the light-colored nests of the open plains beyond. Recently, while collecting ants near Florissant, Colorado, I came upon a colony of three nests of *F. exsectoides* var. *opaciventris*. One of these, near the Colorado and Midland R. R. track, was heavily covered with cinders like the nest cones of *P. occidentalis* above described. Cinders in such situations are, of course, very suitable material for retaining the sun's heat, but it would be going too far to attribute to the ants any knowledge of their value in incubating the brood. Any particles of such a size and shape as to be conveniently carried to the nest, will be collected by these indefatigable insects. At Ash Fork, Arizona, I found some of the cones of *P. occidentalis* covered with the dung-pellets of spermathophiles, and Wasmann has recently observed a similar habit on the part of the European *F. pratensis*, which, in certain localities, covers its nest with the dung-pellets of rabbits and the dried flower-heads of *Centaurea*.

Even more interesting than the dimensions and composition of

the *exsectoides* nests is the fact that they show very clearly some of the conditions which lead to their ultimate decay and abandonment by the ants. Observations made near Scotch Plains, together with those I have collected in some other localities (Staten Island, Highland-on-Hudson, Colebrook, Conn.), show that these structures pass through the following evolutionary and involutionary stages:

1. The incipient nest. In a previous article¹ I maintained that nests of *F. exsectoides* may be established in two different ways: first by the association of a recently fertilized female with workers of her own species from the maternal or some neighboring colony, and the emigration of the company thus formed, followed by the construction of a new nest in a different locality, and second, by the association of a recently fertilized female with an effete or queenless colony of the common black ant (*F. fusca* var. *subsericea*). In the latter case the female remains with the host species until her first brood of workers matures and the host workers have perished. Then, the object of this temporary parasitism having been accomplished, the pure *exsectoides* colony is able to multiply rapidly and without extraneous assistance. In this, the earliest stage in the development of the colony, the nest is, of course, that of *F. subsericea*, a low obscure mound overgrown with long grass and perforated with numerous entrances. Even when the colony is pure from the start, however, that is, when a young female associates herself with workers of her own species, the nest is of this same character as shown in my former paper (*antea*, Pl. XII, Fig. 1). Similar nests were seen in the Scotch Plains colony in close proximity to the large mounds.

2. As the ants keep enlarging their nest it takes on a somewhat different appearance. They deposit large quantities of earth and vegetable detritus on the summit of the mound and kill off the grass in this region, so that the mound comes to have a bare summit and is surrounded by a broad belt of tall grass. This grass belt, to which the numerous openings of the nest are largely confined, is usually thinned out by the ants to admit the sun's light and warmth to the soil in which it grows. Two young nests of this description are represented in my former paper (*antea*, Pl. XIII, Figs. 1 and 2). The grass zone is occasionally retained until the nest reaches a large size. This is the case in the one figured on Pl. LXIII, which is No. 11 of the table on p. 404.

3. Most nests, however, that have attained a large size and are

¹ On the Founding of Colonies by Queen Ants, with Special Reference to the Parasitic and Slave-making Species: Bull. Am. Mus. Nat. Hist., XXII, 1906, pp. 33-105, pll. viii-xiv.

inhabited by colonies or parts of colonies at the acme of their prosperity and development, are completely or almost completely free from grass. There can be no doubt that this vegetation usually succumbs to the sharp mandibles of the ants. A number of nests of this description, appearing as compact earthen mounds, covered only with a small quantity of vegetable detritus, were seen in a large clearing near Scotch Plains. Four of these are shown in Pl. LXIV. They were all smaller than any of those measured for the above table.

4. This stage is characterized by a growth of moss which first makes its appearance in a narrow band around the extreme base of the mound just above a shallow, moat-like depression about 20 cm. in diameter which often encircles the nest and separates it from the surrounding surface. This moss is *Ditrichum pallidum*,¹ a species which is too small and delicate to interfere with the activities of the ants. In the course of time it is partly or completely supplanted by a larger and more vigorous species (*Polytrichum commune*), which begins to form a densely tufted zone around the base of the mound. This moss is rarely found in the woods near Scotch Plains except on the ant-hills, and I was at a loss to account for its singular distribution till Mrs. Britton informed me that it is preëminently a bank-loving species. As the soil of the woods is very level, the plant naturally takes to the only bare elevations in the vicinity. It is not improbable that the *Ditrichum* may in some way prepare the soil for the growth of the *Polytrichum*. Pl. LXV represents the largest nest in the colony (No. 8 of the above table), which had a zone of *Ditrichum* 10-20 cm. broad around its base, but too delicate to show in the photograph. Plates LXVI, LXVII, and LXVIII show that the *Polytrichum* zone continually widens until only a small area at the summit of the mound, the umbilicus, is left uncovered. In Plate LXVII it has invaded a nest which retained a well developed grass zone, but this is evidently destined to disappear before the advancing moss. Nests over which the *Polytrichum* carpet is far advanced are invariably depauperate. The ants are few in number and seem to be rather inactive, a condition undoubtedly attributable to the growth of the moss. This plant has very hard, tough stems and roots, which the ants are unable to sever, so that they cannot dispose of it as they do of grass and other plants. It chokes up the basal zone of entrances, or at any rate grows so densely as to make them

¹For kindly identifying the mosses mentioned in this paper I am indebted to the well known bryologist Mrs. Elizabeth G. Britton.

inaccessible to the insects. The densely tufted moss is much like fur and seriously impedes the insects in going to and from the nest, so that in some nests invaded by the *Polytrichum*, a second zone of entrances had been constructed nearer the summit and along the inner edge of the moss zone. In one of the large twin nests (No. 6) shown in Pl. LXVI the ants constantly made a bridge of a fallen log running from the ground to the umbilicus. It is certain, moreover, that the moss, which absorbs and retains quantities of water and therefore reduces the temperature of its surroundings, must impair the usefulness of the mound as an incubator.

5. The *Polytrichum* carpet continues to grow at its upper edge until it envelops the summit of the mound and extinguishes the ant community. In one mound of this description, with an uncovered area only 20 cm. in diameter, a few lethargic ants still lingered in the earth of the summit; from other similar and older nests they had completely disappeared. While the dense carpet continues to expand, herbaceous, and even woody plants of many species begin to settle on the mounds and eventually in great part completely replace the moss. The mound subsides somewhat, probably owing to the collapsing of its galleries and chambers, and becomes flatter and less conical. It may still be recognized, however, after the lapse of years as was shown by one mound which supported bushes with stems 5-6 cm. in diameter. On these advanced nests at least three other mosses (*Dicranella heteromalla*, *Catherinea angustata*, and *Hypnum recurvans*) may be seen growing singly or in company.

Do the ants emigrate and seek a new nesting site when the invasion of the *Polytrichum* becomes intolerable, or do they gradually die off without deserting the mound which they have reared with such diligent solicitude? This is a difficult question to answer, because a single *exsectoides* colony may extend over several mounds and these may be connected by subterranean galleries. The fact that the ants in mounds invaded by *Polytrichum* have all the appearance of relicts smitten with the weariness and dejection so characteristic of old and depauperate ant communities, certainly favors the view that the insects die off *in situ*.

It is equally difficult at present to answer the question as to the time required to bring about the changes described in the above stages. The age limit of the nest was considered by McCook (*l. c.*, pp. 265-267), who concluded that he had "good reason to believe that some of the hills are at least thirty years old." This estimate is probably as close as any that can be obtained until some one

actually watches the growth of a mound from its inception to its decay.

It would be important to know whether the above stages may be detected in the development of the *exsectoides* nests throughout the range of the species. Incidental remarks in McCook's work seem to indicate that the nests in Pennsylvania present the same peculiarities which I have described. He mentions (p. 254) twenty nests near Warrior's Mark, in Blair County of that State, as "abandoned and covered with moss and grass." And on page 256 he says: "Many a romance of ant life lies hidden within those silent moss-covered mounds." "I have thought that some of these abandoned hills have been reoccupied as they carry a moss-grown and ancient appearance, although in full activity."

For any observations corresponding to those recorded for the Scotch Plains colony it is necessary to turn to the works of European writers. Europe possesses a species of *Formica* (*F. exsecta*) which is not only so like *exsectoides* in color and structure as to have suggested the name of the American species, but is also very similar in some of its habits. These have been studied by Forel,¹ Wasmann,² and more recently by Holmgren.³

F. exsecta lives in bogs and meadows, at lower altitudes in the north but in southern Europe on high hills or mountains. According to Wasmann, "The architecture of the nest is, generally speaking, a small edition of that of the fallow ant (*F. rufa*), both in regard to its dimensions and the materials employed. It consists of much finer substances, dried grass-blades, heather leaves, etc., and contains a much greater admixture of earth. The heaped-up vegetable detritus, so characteristic of all so-called 'ant-hills,' forms in this case only the top; beneath it lies a layer of densely felted grass-stems, grass-roots and soil, in which the true galleries and the chambers of the nest are excavated and whence they extend further down into the earth. The form of the nest is that of a strongly truncated cone. Almost never have I seen nests, either in Vorarlberg or in the Rhineland, with an arched dome like that of *F. rufa*, but almost invariably only such as had a flat top like that of *F. pratensis*. In mountain meadows the cone is sometimes 50 cm. or more in height, its circumference 1 or

¹ Les Fourmis de la Suisse. Zürich, 1874, pp. 191, 192.

² *Formica exsecta* Nyl. und ihre Nestgenossen. Verhand. naturhist. Ver. Rheinl. Westf., 1894, I Heft.

³ Ameisen (*Formica exsecta* Nyl.) als Hügelbildner in Sümpfen. Zool. Jahrb., Abth. f. Syst., XX, 1904, pp. 353-370, 14 text-figs.

even 1.5 m. The cone of the *exsecta* nest is, speaking more precisely a crater, consisting of soil and felted plant growth, filled in at the top with dry vegetable detritus. The nests therefore belong to Forel's 'combination nests,' in which an earthen substructure is combined with a superstructure of plant detritus. The *exsecta* nest is peculiar in having the earthen portion much more extensive than the top and enclosing it like a crater."

The development and decay of the nests of this ant have been studied near Aborrtträsk in Gellivare, Lapland, with results that show a remarkable similarity to the conditions above recorded for the American *exsectoides*, if we make due allowance for the fact that the European ant nests in damp meadows or bogs whereas our American species prefers dryer soil or even hill-slopes covered with open woods.¹

I here reproduce the summary of Holmgren's observations:

"1. The ant-hills in the willow zone are larger, but less numerous than those in the *Sphagnum* zone of the bogs. The greater size depends on the accessibility to more abundant building materials. Their smaller number is likewise attributable to the same conditions, since a greater number of ants are constrained to secure their food and building materials in a relatively small area. Migration for the purpose of founding new nesting sites is unnecessary on a large scale where food and especially building materials are abundant. Access to an abundance of the latter also explains the fact that in the willow zone the nests are not overgrown by *Polytrichum strictum*, for here the ants can inhibit the invasion of the moss by uninterrupted building.

"In the *Sphagnum* zone, however, building materials are scarce and on this account the ant colonies must be smaller and migration occurs on a larger scale. This accounts for the smaller size and greater number of ant-hills in this zone.

"In the damp bog, building materials are relatively very scarce. Here the hills are very much reduced in size and number. Owing to the moisture in this zone there are few spots that will permit the ants to build hills, for these insects require rather dry soil in which to establish themselves.

"2. The position of the hills in damp places prevents the ants

¹There are in America two other forms closely related to *F. exsectoides*, namely *F. exsectoides* var. *opaciventris* Emery and *F. ulkei* Emery. The former is known only from Colorado, where it nests in dry, open situations at an altitude of 6000-8000 ft. Its nest-cones resemble those of the typical *exsectoides* in shape but are covered with pebbles instead of vegetable detritus. *F. ulkei* which is unquestionably a boreal species, was originally described from South Dakota, but I have recently received worker and female specimens from Nova Scotia. Its nesting habits are unknown but probably resemble those of *exsecta* or *exsectoides*.

from establishing any large general trails when they go forth to forage. Where the base of the nest is completely surrounded by water, they are either completely isolated or must climb from leaf to leaf along the plants until they reach *terra firma*. In general, such hills undergo no further additions to their bulk.

"3. Plants are rather quick to gain a foothold on the ant-hills. The first and main vegetation of the nests is *Polytrichum strictum*, which forms a dense carpet. The condition which leads this moss to its invasion is the comparative dryness of the nest. The *Polytrichum* carpet gradually spreads until it completely covers the hill.

"4. The remaining plants that creep up onto the hills usually belong to species growing in the immediate neighborhood. Other plants are rarely found and these grow on the umbilicus or summit which they have reached as seeds and where they have found a place suitable for germination.

"5. The outer form of the ant-hill depends on the carpet of *Polytrichum*. If this moss advances onto the hill from the side, the substance of the nest flows over, so to speak, onto the opposite side. In other words, the ants continue to add to the mound on the uninvasioned side. One observes, moreover, that the nest-substance always spreads in the directions where the moss carpet is least developed. In other words, the ants withdraw as the *Polytrichum* carpet advances.

"6. Owing to the conditions stated in the preceding paragraph, the basal portions of the ant-hill are abandoned by the ants *pari passu* with the advance of the carpet. This takes place step by step. The ants do not leave the basal portions till the carpet has risen too far. This explains why the inhabited portions of the nest extend down deepest into the hill where the diameter of the umbilicus is greatest.

"7. Another result of the invasion of the *Polytrichum* is the pronounced reduction in the number of ants in the hill due to emigration, since they are unable to add to the mound, while its habitable portion is continually growing smaller. These conditions account for the greater number of ant-hills in the zone of *Sphagnum* hummocks.

"8. When the *Polytrichum* carpet has reached a certain height the ants cease to build. This follows directly from the preceding paragraph.

"9. The *Polytrichum* carpet steadily advances till it displaces the ants completely.

"10. The apparent aversion shown by the ants for the inner portions of the hill already covered by the *Polytrichum* is due to the

fact that the moss attracts and retains water, so that these portions become rather moist and therefore unsuitable as a dwelling for the insects.

"11. It follows as a general conclusion from paragraphs 5-10 that there must be between the *Polytrichum* and the ants a severe struggle in which the moss is always victorious.

"12. *Sphagnum* often gains a foothold on the hill before the *Polytrichum* has completely overgrown the summit, or umbilicus. *Sphagnum*, generally speaking, displaces *Polytrichum*. This is certainly the case wherever the *Polytrichum* hills have not been destroyed. From this follows:

"13. The *Polytrichum*-hummocks are converted into *Sphagnum*-hummocks through a displacement of the former by the latter moss; and this is the end-product of the ant-hills.

"The most general conclusion reached in the foregoing paragraphs is that the ants play an important rôle in the formation of hummocks in the bogs under consideration, since the hills serve as growth-foci for the moss and peat vegetation."

Holmgren has also observed that in Lapland the nests of another ant (*F. rufa*) are gradually overgrown by boreal plants (*Vaccinium vitis idæa*, *myrtillus* and *uliginosum* and *Rubus chamæmorus*). In this case also the plants creep upward from the base of the hill, gradually driving the ants to the summit and eventually extinguishing the colony.

According to a footnote in the excellent work of my friend Dr. K. Escherich of Strasburg¹ a struggle between ants and mosses like that recorded by Holmgren and myself seems to occur in certain parts of Germany. He says: "Dr. A. Ludwig brought me from a bog in Grunewald near Berlin a number of dried masses of *Polytrichum strictum*, the basal half of which was perforated with chambers and galleries. The inhabitants of these, a species of *Myrmica*, are driven out by the increasing moisture due to the gradual intrusion of water-storing *Sphagna*." Escherich also mentions similar observations made by Kuhlitz in the bogs of Western Prussia.²

Whether a similar displacement of ants by mosses occurs among such American bog-ants as *Myrmica rubra brevinodis*, which, as I have shown in a former paper,³ nests in hummocks of *Polytrichum commune*, and *Formica cinerea* var. *neocinerea*, which I have found

¹ Die Ameise. Schilderung ihrer Lebensweise. Braunschweig, 1906, 232 pp., 68 text-figs.

² Vorstudien über die Fauna des Betula nana-Hochmoores im Culmer Kreis in Westpreussen Nordd. Wochenschr., n. F. I, 1902, p. 613.

³ Ethological Observations on an American Ant (*Lepthorax Emersoni* Wheeler). Arch. f. Psych. u. Neurol., II, 1903, pp. 1-31, 1 fig.

nesting in large grassy hummocks in meadows from Colorado to Illinois, must be determined by renewed observations.¹

2. THE TENT-BUILDING ANT AND THE PITCHER PLANT.

While engaged in making the observations on the habits of the tent-building ant (*Cremastogaster lineolata*) recorded in a former article² I came upon another instance of maladaptation very different from that described in the preceding paragraphs. The tent-building ant is one of the most plastic and adaptable of our North American Formicidæ. This is shown both in its wide variability over an extensive geographical range and in its ability to construct, often at a considerable distance from its nest, beautiful carton or earthen tents over its herds of aphids and coccids. We should expect such an ant to be more than ordinarily skilful in evading or circumventing the wiles of inimical plants. This, however, seems not to be the case. While examining the pitcher-plants (*Sarracenia purpurea*) in the bogs about Lakehurst, New Jersey, I found the ascidia, or pitchers, in many cases partially filled with the dead remains of *Cremastogaster lineolata pilosa*, a subspecies which seems to be characteristic of boggy spots in the pine barrens. Undoubtedly thousands of workers of this ant are annually destroyed and consumed by these apparently passive insect-eating plants.

The extremely interesting devices whereby the plants of the North American genus *Sarracenia* are able to entrap great numbers of insects, have been described by several botanists, notably by Vogt,³ Hooker,⁴ Mellichamp,⁵ Schimper,⁶ Zipperer,⁷ Macfarlane,⁸ and Meehan.⁹ Macfarlane, especially, has gone into the subject in considerable detail and has given many figures illustrating the development and structure of the pitchers in all the species of *Sarracenia* (*S. flava*,

¹ The Occurrence of *Formica cinerea* Mayr and *Formica rufibarbis* Fabr. in America. Amer. Natur., XXXVI, 1902, pp. 947-952.

² The Habits of the Tent-building Ant, *Cremastogaster lineolata* Say. Bull. Am. Mus. Nat. Hist., XXII, 1906, pp. 1-18, pl. i-vi.

³ Phytohistologische Beiträge, II, Die Blätter der *Sarracenia purpurea* Linn. Sitzber. K. K. Akad. Wien, 1865, I Bd. pp. 281-300, 2 Taf.

⁴ Address to the department of Botany and Zoölogy. Report 44th Meet. Brit. Assoc. Adv. Sci. Belfast (1874) 1875, pp. 102-116.

⁵ *Sarracenia variolaris*. Amer. Natural., XI, 1877, pp. 432-433.

⁶ Notizen über insectenfressende Pflanzen. Botan. Zeitg., 40 Jahrg., 1882, pp. 226-234, 242-248.

⁷ Beitrag zur Kenntniss der Sarraceniaceen. Munich, 1885.

⁸ Observations on Pitchered Insectivorous Plants. Part I, Ann. Botan., 1889-1890, pp. 253-266, pl. xvii; Part II, *ibid.*, 1893, pp. 403-458, pl. xix-xxi.

⁹ *Sarracenia variolaris*. Meehan's Monthly, IV, 1894, p. 1, 2. pls.

drummondi, *rubra*, *variolaris*, *purpurea*, and *psittacina*.¹ While the general structure is the same in all of these, there are interesting differences in detail in the various species. In all the outer surface of the pitchers is furnished with scattered, honey-secreting cells, which Macfarlane appropriately calls "alluring glands," since they attract the insects, especially the ground-loving species, like the ants, and lead them to the orifice of the pitchers. In *S. purpurea* there are small upwardly directed hairs on the outside of the pitchers, while the inside presents a series of surfaces modified in such a way as to lead the insects to their death in the liquid contained in the bottom. For these surfaces Macfarlane has adopted the names proposed by Hooker. The uppermost portion of the pitcher lining, the so-called "attractive surface," is covered with short downwardly directed hairs. Below this there is a smooth slippery surface ("conductive surface") which is succeeded in turn by a densely "glandular surface" not represented in the other species of the genus. And finally the lowermost region presents a "retentive surface" furnished with long downwardly directed hairs. The hairs on the attractive and retentive surfaces prevent the insects from returning to the mouth of the pitcher, while the smooth conducting surface coöperates in offering a very insecure foothold, so that the insects fall into the liquid, usually present in the bottom, and are there eventually digested and in part absorbed by the plant tissues.

The prevalence of ants in the bottom of *Sarracenia* pitchers has been noticed by several observers. Mr. E. Daecke informs me that he has seen these organs of *S. purpurea* half full of dead *Cremastogaster* workers in the bogs near Bamber Station, New Jersey. Riley,² after describing the pitcher of *S. variolaris* of the Southern States, says: "The insects which meet their death in this pitcher comprise numerous species and of all orders; but as one might naturally infer, the ubiquitous, honey-loving ant is the principal victim." And Macfarlane makes a similar observation on our northern form: "I have had the opportunity of examining *S. purpurea* in the New Jersey swamps, and find that the ground-game, notably ants, are largely caught by the pitchers. Flying insects and slugs are not uncommon, and though bulk for bulk they may yield a considerable food supply for the plants, Hooker's supposition [that the pitchers

¹ More recently he has published observations on another species (*S. catesbaei*) from the Southern States (The History, Structure and the Distribution of *Sarracenia catesbaei*. Contrib. Bot. Lab. Univ. Pa., II, 1904, pp. 426-434).

² Descriptions and Natural History of Two Insects which Brave the Dangers of *Sarracenia variolaris*. Trans. Acad. Sci. St. Louis, III, 1874, pp. 235-240, 2 figs.

are especially adapted for catching ground-game] appears correct for this species. In one specimen examined, a large nest of ants had been established in three of the older and rather dry brown leaves, just beneath the reddish green leaves that were actively catching prey."¹

That these insects should actually inhabit the old leaves of a plant whose fresh leaves are so admirably adapted to their destruction, is a reflection on ant "intelligence," especially in view of the fact that some other animals have learned to turn the insect-eating habits of one of the species of *Sarracenia* to their own advantage. Meehan (*l. c.*) cites an observer who has seen birds hanging about the pitchers of *S. variolaris* and even splitting them for the sake of feeding on the entrapped insects, and Riley (*l. c.*) describes the larva of a moth which feeds on the leaves of the same *Sarracenia* and a carrion fly whose larvæ actually develop in the macerating insects at the bottom of the pitchers. The moth is *Exyra semicrocea*. "The egg is laid within the tube and the young larva covers the smooth surface with a fine gossamer-like web, generally closing up the mouth by webbing the lips together. As it increases in size it frets the leaf within, feeding on the parenchyma and leaving only the epidermis. The ochre-colored excrement falls in pellets to the bottom of the tube, where it gathers in a compact mass above the putrid remains of the insects which have been captured before the closing of the mouth. The transformations are undergone in a slight cocoon usually constructed just above the mass of excrement. There are at least two broods of the insect each year, the first larva appearing during the early part of May, the second toward the end of June."² The development of the fly (*Sarcophaga sarraceniæ*) is thus described by Riley: "The mother fly drops her living larvæ within the tube to the number of

¹ On August 20, while the manuscript of this article was being copied for the printer, Miss Delia Marble had the kindness to send me several fine specimens of *Sarracenia purpurea* from a bog near Bedford, New York. The pitchers contained no specimens of *Crematogaster* but instead species of two other genera, namely, several dead workers of a variety of *Formica fusca* near *subaenescens*, two dead females of *Dolichoderus maria*, which does not nest in bogs, and in one of the old and somewhat withered pitchers, a fine living colony of *D. plagiatus pustulatus* var. *inornatus*, a rare ant of which I had never before seen the nest. This colony contained numerous pupæ and winged females. A search through the insect remains in the pitchers on the same and other plants failed to reveal any traces of *inornatus* workers. During September Mr. E. Daecke sent me from Toms River, New Jersey, a small, partially dried pitcher of *S. purpurea* in which he had found a living colony of another ant, *Tapinoma sessile*. Can it be that these ants have learned to exploit the *Sarracenia* without being entrapped?

² More recently Mr. F. M. Jones has published an interesting paper (Pitcher-Plant Insects, Entom. News, XV, 1904, pp. 14-17, pls. iii. and iv.) on the moths that breed in the pitchers of *S. flava*. He enumerates three species (*Exyra ridingsii*, *semicrocea* and *rolandiana*). He also finds that a solitary wasp (*Isodonita philadelphica*) builds its nest in the pitchers.

upward of a dozen, and these easily find their way to the bottom, where they feed on the softer parts of the macerating insects which have accumulated there. As a rule but one of the *Sarcophaga* larvæ matures, the others having fallen victims to its gluttony and superior strength. When full fed, or rather when it has appropriated all the nourishment at hand, this maggot works through the tube (by this time weakened and decayed at the base) and burrows in the ground, where it undergoes its transformations, and whence in a week or more, according to the season, the fly emerges."

A few years ago Dr. J. B. Smith discovered another dipterous insect, a mosquito (*Wyeomyia smithii*) whose larval and pupal stages develop in the liquid of the pitchers of *S. purpurea*.¹ Mr. Daecke writes me that he has found the *Wyeomyia* larvæ near Bamber Station, New Jersey, in pitchers in which so many *Cremastogasters* had been drowned, that he "wondered how they could exist, since the water must have been laden with formic acid." According to Dr. Smith these larvæ do not need to come to the surface of the liquid to breathe, like the larvæ of *Culex*, and even lived "for nearly two weeks under a film of oil which covered the surface of their breeding jar." He also finds that this insect winters in the *Sarracenia* pitchers "in the larval stage, freezing and thawing as often as need be during that season. It pupates late in May and becomes adult a week or ten days later. Eggs are laid in the leaves singly or in small groups; fastened to the sides or floating on the surface. The summer broods mature in about a month, and there are probably three if not four series; but the broods overlap so much that the breeding is practically continuous. Late in the season the adults select the new leaves for oviposition even if they are yet dry."²

It is evident that if the ants had sufficient intelligence to gnaw holes in the walls of the pitchers, they could not only enter and leave these organs at will, but also visit the nectaries and perhaps secure plenty of insect food with impunity. Although *Cremastogaster* has not yet developed this ability, there is no reason to suppose that it may not do so in the course of time. I am led to entertain this possi-

¹ Ent. News, XXII, 1901, pp. 180, 254; Life History of *Aedes smithii* Coq., Journ. N. Y. Ent. Soc., X, 1902, pp. 10-15; see also for a description of the larva: H. G. Dyar, Descriptions of the Larvæ of Three Mosquitoes. Journal of the N. Y. Ent. Soc., IX, 1901, pp. 177-179, pl. x, figs. 1-2.

² The above mentioned insects are by no means the only ones that can live in the *Sarracenia* pitchers. While examining the plants sent me by Miss Marble I found, in addition to the *Wyeomyia* two other fly larvæ that manage to thrive and develop in the digesting insect remains at the bottom of the pitchers. One of these was a *Chironomus* larva, present in considerable numbers in several of the pitchers, the other was apparently a Tipulid larva, of which only a single individual was seen.

bility because Vossler¹ has recently seen some African ants which actually accomplish a similar feat. These insects were very fond of entering the immature flowers of *Cobaea scandens* and cutting away the woolly accumulation of hairs at the base of the bell-shaped corolla in order to reach the nectaries. When Vossler plugged the opening of the corolla with cotton, the ants gnawed holes in the base of the flower and thus attained their end in the directest manner possible.

3. MYRMICA AND THE SUN-FLOWER.

Professor T. D. A. Cockerell has recently called my attention to a third case of maladjustment in the relations of ants to plants. In the neighborhood of Boulder, Colorado, he has repeatedly seen masses

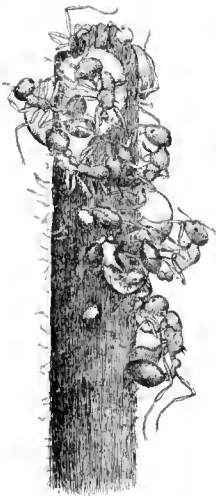


Fig. 1. Broken twig of Sunflower, showing ants (*Myrmica brevinodis*) caught and killed by the exuding sap.

of ants (*Myrmica rubra brevinodis* var.) attracted and killed by the sap that exudes from broken stems and petioles of the sun-flower (*Helianthus annuus*). This plant is very abundant in the lower ground about Boulder, and its sap, as I can testify from personal observation, becomes excessively sticky on exposure to the air, so that an ant that has once touched it with its legs or antennæ is held fast until it perishes. In this case it is difficult to see how the plant can profit by destroying the insects, for the catastrophe is purely accidental, depending on an occasional injury to the plant. A typical specimen showing a number of dead ants partially embedded in the inspissated sap, was kindly forwarded to me by Professor Cockerell and is represented in the accompanying figure. It is interesting as showing on a small scale the way in which ants and other insects became embedded in such substances as amber and copal.

Professor Cockerell surmises that this fatal condition, in which, as in the preceding instances, the ants succumb, may be due to the meeting of two organisms originally belonging to widely separated biogeographical environments; the *Myrmica* being essentially a northern or subboreal species, while the sun-flower represents an austral element which has, during comparatively recent times, invaded the domain of the *Myrmica*. This view, which is certainly

¹Verhinderung des Fruchtausatzes bei *Cobaea* durch Ameisen. Zeitschr. f. wiss. Insekt. Biol., II, 1906, pp. 204-206.

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plausible in this instance, will not, however, apply to the preceding cases, for the *Polytrichum* and *Formica exsectoides* are both subboreal organisms, and the pitcher-plant and *Cremastogaster pilosa* are both of subtropical origin, and there is every reason to believe that these organisms have been associated with each other for long periods of time. It seems natural to suppose that in all the cases described in this article the havoc wrought by the plants is not sufficiently great seriously to impair the vitality of the respective species of ants. In other words, the drain of a heavy annual destruction of individuals or even colonies may be easily borne by organisms capable of reproducing so rapidly and abundantly as these insects.

EXPLANATION OF PLATES.

Photographs of *Formica exsectoides* mounds found near Scotch Plains, New Jersey. The dimensions of the nests are given on p. 404 under their respective numbers.

PLATE LXIII. Nest No. 11, of unusually large size and still retaining the broad basal zone of sparse grass so characteristic of younger nests.

PLATE LXIV. Four nests (not included in the table on p. 404) from a group of several in a clearing. These nests had been denuded of all grass by their ant inhabitants.

PLATE LXV. Nest No. 7, the largest of the colony. It was surrounded by a zone of moss (*Ditrichum pallidum*) which, however, does not show in the photograph.

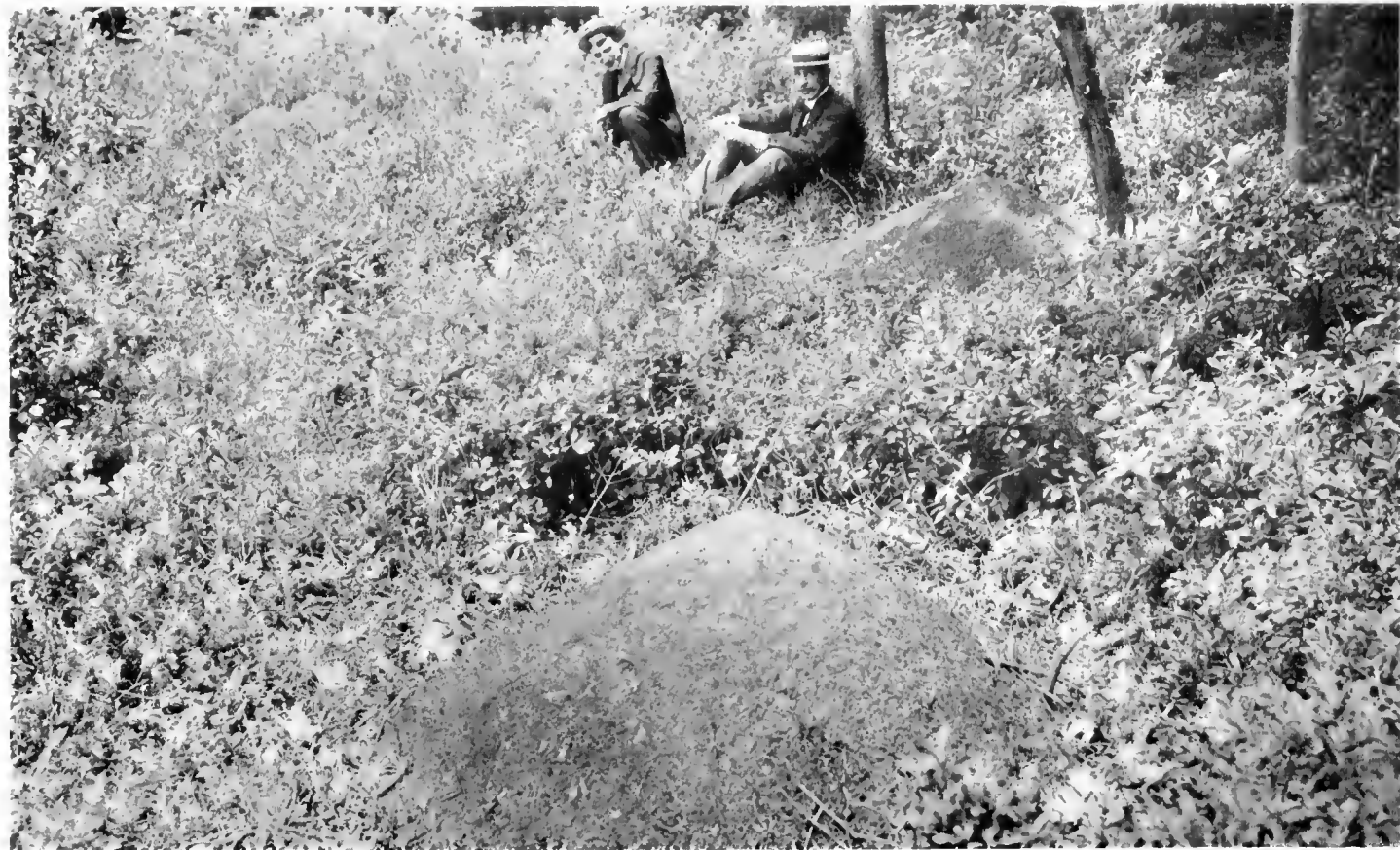
PLATE LXVI. Twin nests invaded by moss (*Polytrichum commune*). The one in the foreground is No. 6 of the table on p. 404.

PLATE LXVII. Nest No. 10, showing the zone of *Polytrichum* advancing and extinguishing the grass zone of an earlier stage (conf. Plate LXIII).

PLATE LXVIII. Nest No. 8, showing the *Polytrichum* zone far advanced toward the summit, or umbilicus, which it will eventually cover.



LARGE NEST OF *Formica exsectoides* WITH GRASS-ZONE.



DENUDED NESTS OF *F. exsectoides*.



LARGE *F. exsectoides* NEST WITH ZONE OF *Ditrichum pallidum*.



TWIN NESTS OF *F. exsectoides* WITH ZONES OF *Polytrichum commune*.



NEST OF *F. exsectoides* WITH ZONES OF GRASS AND *Polytrichum*.



NEST OF *F. exsectoides* WITH ADVANCED *Polytrichum* ZONE.